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Lifespan and age, but not residual reproductive value or condition, are related to behaviour in wild field crickets

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Abstract

Individuals frequently show long-term consistency in behaviour over their lifetimes, referred to as "personality." Various models, revolving around the use of resources and how they are valued by individuals, attempt to explain the maintenance of these different behavioural types within a population, and evaluating them is the key for understanding the evolution of behavioural variation. The pace-of-life syndrome hypothesis suggests that differences in personalities result from divergent life-history strategies, with more active/risk-taking individuals reproducing rapidly but dying young. However, studies of wild animals provide only limited support for key elements of this and related hypotheses, such as a negative relationship between residual reproductive value and activity. Furthermore, alternative models make divergent predictions regarding the relationship between risk-taking behaviours and variables consistent in the short-term, such as condition. To test these predictions, we regularly measured willingness to leave a shelter and the activity level of wild adult field crickets (*Gryllus campestris*) at both short and long intervals over their entire adult lives. We found some support for a pace-of-life syndrome influencing personality, as lifespan was negatively related to willingness to leave the shelter and activity. Crickets did not appear to protect their "assets" however, as estimates of residual reproductive value were not related to behaviour. Although there was considerable variance attributed to the short-term consistency, neither trait was affected by phenotypic condition, failing to support either of the models we tested. Our study confirms that behaviours may covary with some life-history traits and highlights the scales of temporal consistency that are more difficult to explain.

KEYWORDS
behavioural type, Gryllus, life history, pace of life, personality

1 | INTRODUCTION

Behaviour differs among species, among populations of the same species and among individuals within the same population (Wilson, 1998). This among-individual variation in behaviour, aka "animal personality" (Dall, Houston, & McNamara, 2004), has received extensive theoretical and empirical interest in the last two decades, with a range of suggested evolutionary and ecological consequences (Wolf & Weissing, 2012). Among-individual differences, which are contingent on limited individual flexibility, are widespread (Bell, Hankison, & Laskowski, 2009) and linked to fitness (Smith & Blumstein, 2008). As selection is expected to purge less-fit phenotypes, there must be evolutionary

forces maintaining variance in individual behaviour across generations (Dingemanse & Wolf, 2010; see also: Duckworth, 2010; Sih et al., 2015).

Many models for the evolution and maintenance of personality revolve around how individuals value and use resources. If organisms have limited resources, then they are expected to trade off their allocations to survival- versus reproduction-based life-history traits. Allocation to certain traits complements allocation to others, creating divergent life-history strategies within a population, ranging from "fast" (rapid growth, early maturity, short lifespan) to "slow" (slow growth, late maturity, long lifespan). Animals are unable to switch between strategies during their lifetime, but different strategies achieve the same fitness, hence maintaining variation in the population (Mangel & Stamps, 2001). This supposed integration of different traits is known as the "pace-of-life syndrome" (POLS) hypothesis. The *extended* POLS hypothesis predicts that animals' behaviour is integrated into these syndromes (Biro & Stamps, 2008; Stamps, 2007); for example, "fast" individuals are expected to be more aggressive, while "slow" individuals are expected to show slow, but thorough exploration (Hall et al., 2015). Certain behaviours complement certain strategies, with a mismatch between behaviour and life-history strategy leading to reduced fitness (Réale et al., 2010). The absence of a single adaptive peak of behaviour, therefore, allows personality differences to persist in the population.

Individuals may not possess the same amount of resources. Differences in resources are predicted to lead to differences in behaviour by (at least) two models. The first of these, Clark's (1994) "asset protection principle," further developed in a model by Wolf, van Doorn, Leimar, and Weissing (2007a), assumes that individuals possess different body conditions and/or residual reproductive values (RRVs) due to their differing levels of resources. Individuals with a high RRV/condition will be consistently cautious, so that they do not die young and hence fail to expend resources that they had allocated to reproduction later in life (Wolf et al., 2007a). In contrast, low resource individuals, with a low RRV/condition, have limited assets to protect and so will be risk-prone to secure some reproductive success. This suggests that individuals will be either risk-prone, low condition and low RRV, or risk-averse, high condition and high RRV, integrating behaviours and life-history strategies in a similar way to the POLS hypothesis (Wolf et al., 2007a). Indeed, in some cases, traits such as condition and RRV might also be thought to be part of the POLS, if "slow" individuals maintain a higher body condition throughout their lives or their RRV is consistently higher as they do not mate much when young; hence, the two theories are not mutually exclusive. Also similar to the POLS hypothesis, different strategies are thought to have equal fitness pay-offs (Wolf et al., 2007a). There is, however, debate as to whether this mechanism is likely to lead to long-term differences in behaviour, as caution can prevent the accumulation of resources, leading to a depletion of resources in cautious individuals and so leading to them becoming risk-prone, eliminating any consistency in behaviour (McElreath, Luttbeg, Fogarty, Brodin, & Sih, 2007; Wolf, van Doorn, Leimar, & Weissing, 2007b).

Alternatively, individuals may adjust their behaviour continually, based on "state" variables such as current motivation, condition or future fitness expectations (Houston & McNamara, 1999), but in a way that leads to divergence of behaviour, and so consistent among-individual differences. For instance, current body condition may influence risky behaviours such as willingness to feed (David, Auclair, Giraldeau, & Cezilly, 2012) or tolerance of predator proximity (Seltmann et al., 2012). These short-term differences in risk-taking tendency, based on elements of state such as condition or RRV, can lead to long-term differences in behaviour among individuals (Sih et al., 2015). Higher condition/RRV individuals may appear to take more risks, as they are more capable of dealing with the consequences of, for example, allowing a predator to approach more closely (Martín, de Neve, Polo, Fargallo, & Soler, 2006). This allows them to accumulate more resources and therefore stay in better condition or maintain a high mating rate, thus maintaining long-term differences in behaviour (see Luttbeg & Sih, 2010). In this model, resource accumulation and behaviour positively feedback on each other, rather than the unidirectional relationship implied by the models above. We term this the "state-dependent safety model" and base its predictions on the model of Luttbeg and Sih (2010). This is, however, controversial, as it is commonly thought that better condition individuals should take *less* risks, due to their higher RRV (Dammhahn, 2012; Hall et al., 2015; Hawlena, Pérez-Mellado, & Cooper, 2009; Seltmann et al., 2012).

These theories rely either on limitation in resources forcing individuals to trade off allocation to different fitness-related functions or on variation among individuals in resources leading to different strategies, as well as on predation to potentially punish risk-taking individuals. These factors are typically absent in laboratory studies. Therefore, tests of these hypotheses should take place on wild-living animals, in the presence of all the factors that the observed among-individual variation in behaviour has evolved with (Niemelä & Dingemanse, 2014). However, many of the fundamental aspects of these competing hypotheses have not been demonstrated directly; rather, proxies for RRV, such as remaining lifespan, have been used. Furthermore, they do not tend to be simultaneously evaluated in the same population. This requires the capture and identification of wild individuals, and regular measurement of their level of risk-taking, accumulation of mating success and their life-history trajectory. Furthermore, some of these models require selection on mean behaviour to be absent to maintain behavioural variation (POLS, asset protection), while others allow fitness differences between personality types (state-dependent safety), yet confirming this requires estimates of fitness in the wild: a challenging task.

We aimed at testing the POLS hypothesis, the related predictions of the asset protection principle as found in Wolf et al.'s (2007a) model and the predictions of state-dependent safety, following Luttbeg and Sih's (2010) model, using a population of wild field crickets (*Gryllus campestris*). We used video cameras to monitor the population of uniquely identified individuals over their entire adult lifetimes, regularly testing their behaviour and recording their mating successes. We predicted that (i) if behaviour

was related to life-history traits as predicted by the POLS hypothesis, we would see negative relationships between lifespan and behaviours involving being active or taking risks; (ii) if individuals protect their assets as predicted by Wolf et al.'s (2007a) model and to a lesser extent by the POLS hypothesis, RRV and body condition should be negatively related to active/risk-taking behaviours; (iii) alternatively, following the state-dependent safety model based on Luttbeg and Sih (2010), condition and RRV should be positively related to activity/risk-taking; and (iv) mean behaviour will not be related to fitness (following the POLS and Wolf et al.'s (2007a) version of asset protection) or more risk-taking lifestyles give higher fitness (state-dependent safety).

2 | MATERIALS AND METHODS

2.1 | Study subjects

The study was carried out at the "WildCrickets" project field site in Northern Spain in 2013 (see (Rodríguez-Muñoz, Bretman, Slate, Walling, & Tregenza, 2010) and www.wildcrickets.org for further details). *G. campestris* is univoltine, and adults are active in the months April–July following overwintering as nymphs in burrows they dig themselves. At the start of this adult activity period, we randomly placed 120 video cameras over burrows with nymphs, allowing us to record the emergence date and subsequent behaviour of adult crickets. These cameras record 24 hr a day using infrared light at night. If a burrow monitored by a camera is observed not being used by a cricket for several days, we moved the camera to a burrow where a cricket has recently been observed. Migration to and from neighbouring fields is very limited as a result of surrounding unsuitable habitat and barriers to dispersal on all sides of the meadow (Bretman, Rodríguez-Muñoz, Walling, Slate, & Tregenza, 2011).

2.2 | Data collection

We watched the video recordings to catalogue cricket behaviour such as movement among burrows, mating (successful matings were identified when transfer of a spermatophore was visually confirmed), fighting and predation events. Individuals were observed for 57.8% ± 28.9% ($\bar{x}$ ± standard deviation) of their adult lifespan. The vast majority of important events that crickets engage in (mating, fighting, singing, avoiding predators and oviposition) take place at burrows, so we are confident that we captured most of the relevant behaviour (Rodríguez-Muñoz et al., 2010). To complement the video recordings, we directly observed burrows without a camera in the field for the presence of crickets and their identity on a daily basis. As crickets rarely move among burrows as late-instar nymphs, this allowed us to determine emergence dates for individuals at burrows without cameras by recording when an adult was observed where previously there had been a nymph. Crickets were tagged 3 or 4 days (3.76 ± 2.81) after they emerged. We blocked the burrows while tagging or assaying the crickets trapped from them, to prevent other animals, including other crickets, from moving in. If a cricket's death was not directly observed, its death date was set as the day after it was last observed.

2.3 | Behavioural trials

Once caught, we weighed the crickets and carried out behavioural tests to assay their tendency to take risks and activity level. Tests occurred in a temperature-controlled room (19.8°C ± 0.59), in a clear plastic box (290 × 201 × 212 mm) monitored from above by a camera. Crickets were tested twice each time they were caught, with a 30-min interval between tests, to quantify the short-term consistency. Crickets were placed in an opaque tube (80 × 20 mm), simulating a refuge like a cricket burrow, and placed in individual boxes. Using iCatcher, a digital video recording software (www.icode.co.uk), eight virtual trip wires were set across each box, each covering a different area of the box.

As a measure of willingness to take risks, we recorded whether the cricket left the tube or not and how long it took if it did, up to a maximum of 30 min, after which we terminated the trial. If it left the tube, activity was then quantified as the number of virtual trip wires a cricket crossed (see Fisher, David, Tregenza, and Rodriguez-Munoz (2015) for further details on the experimental set-up). This assay predicts activity level in the wild (Fisher, James, Rodriguez-Munoz, & Tregenza, 2015). Furthermore, crickets do not appear to become habituated to the test; capture number was not an important predictor of activity in previous analyses (Fisher, David, et al., 2015). If an individual did not leave the tube within 30 min (41% of trials), a missing observation for activity was recorded. Removing these low activity trials will upwardly bias the estimated mean activity levels of inactive individuals (instead of getting a low activity score they get no score). However, we felt that this was preferable to giving a cricket that did not emerge the minimum activity score, as this would inflate individual repeatability scores if a cricket did this consistently.

The first time an individual was caught, and after the behavioural tests had finished, we fixed a small waterproof vinyl tag to its thorax using cyanoacrylate glue (Rodríguez-Muñoz et al., 2010). Each tag had a unique code, allowing individual identification without disrupting natural behaviour. We also took photographs of the crickets from above and used ImageJ (Schneider, Rasband, & Eliceiri, 2012) to measure the width of the widest part of their thorax. Crickets were then released back to the burrows we trapped them from. Subsequently, we recaught, reweighed and retested (twice each capture) each individual cricket continually at time intervals of around 10 days and continued until the individual was no longer observed alive, allowing us to quantify the long-term behavioural consistency. Quantifying both short- and long-term consistencies is rarely made (but see: David, Auclair, & Cézilly, 2012), yet it is useful as it gives insight into the scales of behavioural variation we are least able to account for.

2.4 | Data analysis

We built two generalized linear mixed models in R (version 3.4.1; (R Development Core Team 2016)) using the package "MCMCglmm"

(Hadfield, 2010). The "out model" analysed whether the cricket left the tube or not as a binary response. The "activity model" examined the movement once the cricket left the tube using the number of trip wires it crossed. In 41% of cases, the cricket never left the tube and so did not record an activity score. The out model, therefore, allows us to include all trials in the analysis, and we can then compare results with the subset of trials where a cricket did leave the tube in the activity model, to check whether the results are broadly in the same direction. The out model used a categorical error structure (used when the response variable is an ordered categorical variable) and had the residual variance fixed to 1, as in binary models the residual variance is defined by the intercept. The activity model used a Poisson's error structure and included the log of the number of seconds the cricket was outside of the tube as an offset, effectively modelling activity as a rate. For both models, we included two random effects: individual identity and the unique combination of individual identity and capture number. Each level of this latter term contains two measures for tendency to leave the tube, as crickets were tested twice each capture, but 0–2 measures for activity, as a measure is only recorded if the cricket left the tube. The variance attributed to individual identity is interpreted as the among-individual, among-capture variance, and so consistency across adult lifespans, and so the individual-capture number effect quantifies within-individual, among-capture variation, and so short-term consistency.

Both models included the same set of fixed effects, aside from the offset, which only appeared in the activity model. These were individual age (days), lifespan (based on when last seen with our network of video cameras), RRV (the proportion of the individual's lifetime matings that occurred after the date of that behavioural test), sex (a two-level factor), the sex–RRV interaction (as other work has found relationships between behaviour traits and reproductive potential in only one of the sexes; e.g., Dammhahn, 2012), condition (mass (g) of the cricket at that capture divided by the width of its thorax), the temperature of the laboratory (°C), an age x temperature interaction (as previous analyses have indicated that age x weather interactions can influence behaviour; Fisher, David, et al., 2015, Fisher, James, et al., 2015)) and estimated lifetime mating success (LMS; the total number of matings an individual was observed to have, divided by the proportion of its lifespan it was under observation) as a fitness proxy. Crickets of both sexes that have more matings have a higher number of offspring surviving to adulthood (Rodríguez-Muñoz et al., 2010); hence, this is an imperfect, but workable proxy for fitness. The term for individual age models the within-individual age–behaviour relationship, so individual crickets become more or less willing to leave the tube, or more or less active, as they age. The lifespan term then models the effect of selective disappearance: if crickets that are more willing to leave the tube or are more active, live less long; van de Pol & Verhulst, 2006). We note that the direction of causality between behaviour and both lifespan and LMS is likely reversed (behaviour influences lifespan and/or fitness) compared to what our regression implies (fitness and/or lifespan influences behaviour). Given this is an observational study, we can only identify associations, not causality, and so another regression with lifespan or LMS as a response variable would not inform us any more about the relationships between behaviour, fitness and lifespan.

Each continuous variable was mean-centred and transformed to unit variance, so all were on the same scale, enabling the effect sizes to be directly compared (Hunt, Brooks, & Jennions, 2005; Schielzeth, 2010). We excluded all crickets that were observed for less than 300 min in total in the field. This removes individuals for which our information is likely to be relatively inaccurate. For the out model, we used an inverse-gamma prior for both the individual and individual-capture variances (V = 1, nu = 0002). For the activity model, we set inverse-gamma priors for all variances. We used 300,000 iterations, with the first 50,000 discarded (burn-in) and then 1/10 subsequent iterations kept (thinning), to estimate parameter effects. A Heidelberger and Welch's convergence test indicated that this chain was of sufficient length (Heidelberger & Welch, 1983). Three model runs were performed to confirm convergence of parameters, with the trace plots inspected to confirm that the correlations between iterations were minimal. We estimated repeatability among individuals over their lifespan and within individuals and among captures, following Nakagawa and Schielzeth (2010), while to determine the overall fit of the models to the data, we calculated the conditional R^2 values (the proportion of total variance explained by both the fixed and random factors) for both models, following Nakagawa and Schielzeth (2013).

3 | RESULTS

We monitored 137 different individuals in the wild for a mean of 408 hr each and also measured their behaviour in the laboratory. Individuals were captured between one and five times (2.54 ± 1.43), giving 587 trials for whether they left the tube or not. Individuals recorded between 2 and 10 measures for willingness to leave the tube ($\bar{x}$ ± SD = 4.28 ± 1.76). For activity, there were 124 unique individuals and a total of 350 assays of activity. Individuals recorded between 1 and 7 activity measures each (2.82 ± 1.47, 22 individuals recorded only a single activity score).

The fixed-effect estimates from the out model are illustrated in Figure 1a. Individuals were more willing to leave the tube as they aged, and individuals more willing to leave the tube had shorter lifespans (Figure 2a). RRV and its interaction with sex were not related to tendency to leave the tube. High-fitness and high-condition individuals were not more or less likely to leave the tube. All other fixed effects had 95% credible intervals (CRIs) that crossed zero. The among-individual repeatability for tendency to leave the tube was 0.046 (0.009–0.256) (mode and 95% CRIs), while the within-individual, among-capture repeatability was 0.558 (0.350–0.732). The conditional R^2 was 0.681.

The fixed-effect estimates from the activity model are illustrated in Figure 1b. Individuals were more active as they aged, and more active individuals had shorter lifespans (Figure 2b). RRV and its interaction with sex were not related to activity. High-fitness and high-condition individuals had similar activity levels. All other

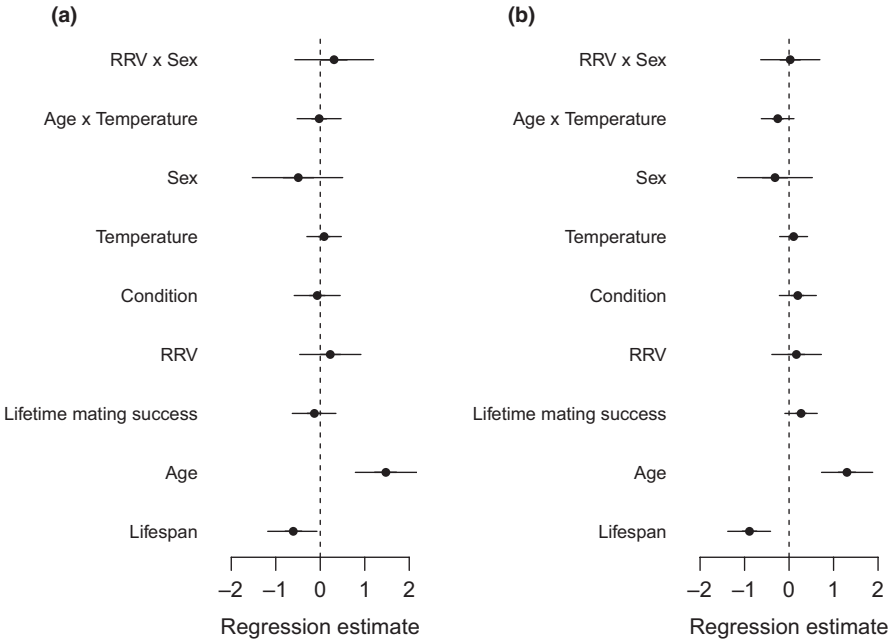

FIGURE 1 Coefficient plot showing the mean and 95% credible intervals for the posterior distributions of the regression estimates for the fixed effects in the out model (a) and the activity model (b). Each continuous variable was transformed into the same units, so the effect sizes are directly comparable. For sex, female was set as the default with males modelled as the contrast, so the effect size indicates the mean difference of males from females. Drawn using coefplot2 (Bolker, 2012)

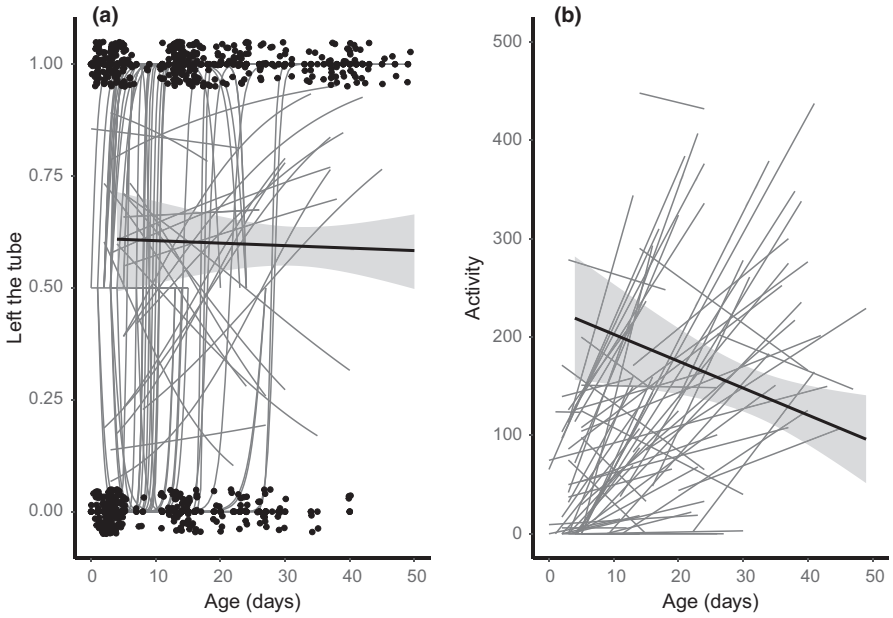

FIGURE 2 Individuals became more willing to leave the tube (a) and were more active (b) as they aged (grey lines, a single regression line fitted through all an individual's measures), while at the population level, there was selective disappearance of the individuals most willing to leave the tube (a) and of the most active individuals (b), so they had shorter lifespans (black line with standard errors). Individual points are shown for tendency to leave the tube, with a small random addition or subtraction, to aid viewing. Drawn using ggplot2 (Wickham, 2009)

fixed effects had 95% credible intervals (CRIs) that crossed zero. The among-individual repeatability of activity was 0.001 (<0.001–0.167), while the within-individual, among-capture repeatability was 0.310 (0.173–0.447). The conditional R^2 was 0.458.

4 | DISCUSSION

4.1 | Initial support for a pace-of-life syndrome

Shorter-lived crickets were more likely to leave the tube and were more active if they did so. This is in line with our prediction (1) following the POLS. This indicates that at least one aspect of a cricket's life history is related to its behaviour. We would need to more thoroughly assess the relationships between different behaviours and other life-history traits to confirm the full extent of this integration. In some formulations, traits such as RRV or condition might be considered to be part of a POLS; for example, "slow" individuals might have consistently higher body condition or maintain a higher RRV longer, but we did not find this. While some previous works have found relationships supporting the predictions of the POLS (Adriaenssens & Johnsson, 2011; Dammhahn, 2012; Dosmann, Brooks, & Mateo, 2015a; Hall et al., 2015; Hawlena et al., 2009; Montiglio, Garant, Bergeron, Dubuc Messier, & Réale, 2014; Niemelä, Dingemanse, Alioravainen, Vainikka, & Kortet, 2013; Niemelä, Lattenkamp, & Dingemanse, 2015), such predictions are not always confirmed (David, Pinxten, Martens, & Eens, 2015; Kluen,

Siitari, & Brommer, 2013; Montiglio, Garant, Pelletier, & Réale, 2014; Réale, Martin, Coltman, Poissant, & Festa-Bianchet, 2009). One possible explanation for variation among studies is the extent to which the behaviours assayed in each system differ from the theoretical concept of "risk-taking" or "activity" which are employed in the POLS and similar hypotheses. In these hypotheses, the measured trait must allow an individual to choose to undertake a risky behaviour, rather than measure the response to a threatening or novel stimulus. Our behavioural measures are clearly proactive, but may incorporate some aspects of response to novelty, as the tube and the box would have been novel to the crickets (at least in the first trial). It may be that reactive behaviour falls along a different axis of variation that is not related in the same way to RRV or condition, but still is related to lifespan. Ultimately, the extent to which our particular measure of activity exactly reflects the theoretical concept which various models expect to be related to state or a life-history strategy remains moot.

4.2 | Behaviour does not depend on residual reproductive value or condition

We found no relationships between RRV and condition, failing to support either the models based on the asset protection principle (prediction 2, Clark, 1994; Wolf et al., 2007a) or models of positive feedback between condition and behaviour (prediction 3, Luttbeg & Sih, 2010). Other studies have mixed results, with both the presence and absence of correlations between behaviour and condition at the among- and within-individual level (Dosmann, Brooks, & Mateo, 2015b; Ferrari et al., 2013; Kluen et al., 2013). For example, chinstrap penguin chicks (*Pygoscelis antarctica*) allow predatory birds to approach them more closely and flee shorter distances when they are healthier (Martín et al., 2006). To allow accurate cost/benefit analysis, decisions individuals make at each time point are predicted to include considerations of their state (Houston & McNamara, 1999), as if state variables feature in many key models for the evolution and maintenance of personality differences among individuals (Sih et al., 2015). However, when definitions for state read: "all those features that are strategically relevant, i.e. features that should be taken into consideration in the behavioural decisions in order to increase fitness" (Wolf & Weissing, 2010), identifying which measurable variables should relate to behaviour in the way predicted by different models may be quite difficult. Here at least, we find a cricket's mass-to-width ratio to not represent a "strategically relevant" feature. Possibly, factors such as whether the cricket has fought recently (which influence circulating hormone levels (Rillich & Stevenson, 2011)), or mated recently, would be more pertinent state variables than condition. Furthermore, adaptive relationships between behaviour and abstract constructs such as RRV require the information about an individual's RRV to be reliable, but if mating success is determined by interactions with others and by stochastic events, then the reliability of any such information may be quite low.

We also found no interaction between RRV and sex, suggesting that the sexes do not value future reproduction differently. Previous research on grey mouse lemurs (*Microcebus murinus*) found a relationship between future reproductive investment and risk-taking only in males (Dammhahn, 2012). Studies on more species are, therefore, required to determine whether sex differences in the POLS are dependent on the mating system or some other form of sexual selection, as sexual selection can both generate and maintain among-individual differences and within-individual consistency (Schuett, Tregenza, & Dall, 2010).

Age was positively related to the activity level. We have previously interpreted this increase in a risky behaviour as a response to lower RRVs in old age (Fisher, David, et al., 2015). However, this study demonstrated the age effect to be independent of a drop in RRV (as we measured it). Instead, crickets may increase in robustness with age, allowing them to take greater risks. Crickets may also be more willing to expend energy as they age, perhaps as mortality causes the population density to drop over time, necessitating greater amounts of movement to acquire matings. This increase in activity and willingness to leave the tube should not have been related to external temperature, as we both restricted this experimentally and modelled its influence statistically.

4.3 | No relationships between behaviour and fitness

More active crickets and those more willing to leave the tube did not have different estimated LMSs, indicating that neither behaviour is under directional selection. Different behavioural strategies giving equal fitness (prediction 4) are required by Wolf et al.'s (2007a) model and earlier, analogous models for the maintenance of life-history variation (Mangel & Stamps, 2001), as otherwise less-fit strategies would be purged from the population. Fitness differences are, however, allowed with Luttbeg and Sih's (2010) model, as behaviour difference arises from positive-feedback loops, rather than stemming from underlying genetic differences in life-history strategy. Our results are, therefore, better aligned with the models of Mangel and Stamps (2001) and Wolf et al. (2007a), suggesting that what maintains a range of strategies in our population is that they have equal fitness benefits. This is in spite of the fact that more active crickets have shorter lives. Evidently, they are able to compensate for this by accumulating as many matings in their short life. We have assumed here that mating success over the cricket's life is a valid proxy for fitness, as previous work indicates that this is true for both males and females in this population (Rodríguez-Muñoz et al., 2010).

We note that there was a relatively limited degree of consistency among individuals over their lifespans. Given that lifespan (a single value for each individual) was related to behaviour, there is enough consistency over this time frame to relate behaviours to variables effectively stable over an individual's life. It was, therefore, possible that a stable life-history strategy could have been related to behaviour over the adult lifespan. More obviously, there was a large amount of consistency within individuals and among captures. This may have been taken as evidence of different personalities if we had

not measured crickets over their entire adult lifespan, rather than a short period of time, as is more common in studies of long-lived vertebrates.

5 | CONCLUSIONS

We found that two behavioural traits were related to lifespan, but not to RRV, providing some support for the POLS hypothesis, but none for the asset protection principle or state-dependent safety. Beyond the associations with lifespan, there was a limited long-term behavioural consistency. There was, however, an appreciable short-term consistency, which was not related to estimates of condition. Identifying the "state" or other variables that do account for this short-term consistency, that are most relevant to our study organism is an outstanding challenge. Ours is the first attempt to measure the parameters of risk-taking, activity, mating success and life history in a wild invertebrate (but see Niemelä et al. (2015) for an analogous boldness–lifespan trade-off in another wild cricket population). In general, invertebrates are grossly under-represented in studies on the behavioural ecology of wild animals, stemming from the difficulty in identifying and tracking individuals who are very small, yet are very commonly used in laboratory studies. Making the effort to study invertebrates in the wild at the individual level is, therefore, essential to ensure that theories and models are not evaluated based on the evidence from a minority of taxa.

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DATA ACCESSIBILITY

Data used for this manuscript and R code to repeat the analysis are available online through Open Research Exeter.

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